Responses of a Rocky Shore Gastropod to the Effluents of Predatory and Non-predatory Crabs: Avoidance and Attraction

PETER B. MARKO[1] AND A. RICHARD PALMER[2]

Department of Zoology, University of Alberta, Edmonton, Alberta T6G 2E9 and Bamfield Marine Station, Bamfield, British Columbia V0R 1B0 Canada

Abstract. Laboratory experiments revealed that the rocky shore gastropod, *Nucella lamellosa* (Gmelin), could discriminate between the effluents of predatory and non-predatory crabs. *N. lamellosa* turned away from seawater that had passed over the large predatory crab, *Cancer productus* Randall. This avoidance behavior was observed in snails from two localities that, based on differences in shell form, presumably experienced different levels of predation intensity. The scent of the non-predatory crabs *Pugettia producta* (Randall) and *Lopholithodes mandtii* Brandt had no effect on the turning behavior of snails from either site. Surprisingly, snails from both sites were attracted to the scent of a small shore crab, *Hemigrapsus nudus* (Dana), but moved at random in response to a common prey item *Balanus glandula* Darwin.

These results suggest that *N. lamellosa* can assess from a distance the relative risks posed by different species of crabs, and respond appropriately. The unexpected attraction to *H. nudus* suggests that *N. lamellosa* may use this effluent to home in from a distance on potential refugia, because *H. nudus* are often associated with crevices and the undersides of boulders where *N. lamellosa* would be less vulnerable to larger predators.

Introduction

Many marine invertebrates exhibit escape and avoidance behaviors (Bullock, 1953; Gore, 1966; Phillips, 1975; Lawn and Ross, 1982; Palmer *et al.,* 1982; Miller, 1986). An escape behavior is a response to direct contact

with a predator and may be mediated by both physical and chemical stimuli, while an avoidance behavior is exclusively a response to substances diffused from a predator (Phillips, 1977). Hence, an avoidance behavior is a response to a distant threat, and may be adaptive for slow moving organisms that cannot otherwise escape from imminent attack by a faster moving predator.

Marine gastropods exhibit both escape and avoidance behaviors (for reviews see Kohn, 1961; Feder and Christensen, 1966; Ansell, 1969; Mackie, 1970; Snyder and Snyder, 1971; Feder, 1972). However, these responses are usually to slow-moving asteroid and gastropod predators (*e.g.,* Hoffman *et al.,* 1978; Fishlyn and Phillips, 1980; Schmitt, 1981), and few have involved predatory crabs [except see Geller (1982)]. Although predator-specificity of avoidance behaviors has been examined in some gastropods (Edwards, 1968; Phillips, 1976, 1977; Hoffman, 1980), the specificity of responses to highly mobile predators has not been investigated. In addition, few studies have tested for differences in responsiveness among populations experiencing different predation pressures.

The recent discovery that the scent from predatory crabs can influence the rates of feeding and growth, and the shell morphology of two thaidine gastropods, the northeastern Pacific *Nucella lamellosa* (Gmelin) (Appleton and Palmer, 1988) and the North Atlantic *N. lapillus* (L.) (Palmer, 1990), raises an important question. To what extent are these responses specific to predatory crabs rather than a more generalized response to crab effluents? A second question we addressed was whether snails from populations that had experienced different predation regimes exhibited different specificities or magnitudes of avoidance behaviors.

Materials and Methods

Collection sites

Nucella lamellosa individuals were collected from two sites in the vicinity of Bamfield, Vancouver Island, British Columbia, during the summers of 1989 and 1990: (a) Grappler Inlet (48° 50′ 00″ N, 125° 06′ 49″ W), a quiet estuarine bay that receives little or no exposure to breaking waves; and (b) the Ross Islets (48° 52′ 24″ N, 125° 37′ 38″ W), a group of small islands in Barkley Sound that experiences intermediate wave action. With one exception, fresh snails were collected for each trial during low tide and held in air in the main aquarium room at the Bamfield Marine Station until used later the same day. However, one series of 100 snails from Grappler Inlet ('Grappler-lab') was acclimatized in running seawater for four days with *ad libitum* food (*Balanus glandula* Darwin on small stones). In all trials, snails were used only once and then returned to their site of origin. Care was taken not to collect again from the same area on the shore.

The effluent sources were acclimatized in the laboratory for four to five days after collection. In total, 4 *Cancer productus* Randall, 40 *Hemigrapsus nudus* (Dana), 9 *Pugettia producta* (Randall), 1 *Lopholithodes mandtii* Brandt, and approximately 600–900 *Balanus glandula* on small stones, were used as stimuli. Only male crabs were collected and were weighed wet in air. Because of large differences in body size, we could not precisely standardize the weights of crabs or barnacles in different trials. *C. productus* and *P. producta* individuals were collected from Grappler Inlet, *H. nudus* individuals from Dixon Island (48° 50′ N, 125° 06′ W), and the single *L. mandtii* from near Wizard Islet (48° 51′ N, 125° 09′ W). All crabs were offered frozen fish (sole and flounder) and blades of kelp (*Macrocystis* spp.) while held in the laboratory. *C. productus* and *H. nudus* consumed the fish; only *P. producta* ate kelp. The *L. mandtii* did not eat any food but was retained for only one week.

Experimental procedure and rationale

Nucella lamellosa specimens were exposed to effluents in a choice apparatus similar to that used by Pratt (1974). Two plastic holding tanks [Fig. 1a(i), 20 × 15 × 18 cm] supplied by a common seawater source each emptied into separate plastic header tanks [Fig. 1a(ii), 30 × 40 × 10 cm]. The header tanks overflowed onto inclined, textured glass plates that sloped toward each other [Fig. 1a(iii), 25 × 35 cm] and met at a central horizontal platform of plexiglass [Fig. 1a(iv)]. Seawater from the two sides only mixed on the center platform and drained from there via small holes (Fig. 1b). The flow rates into both holding tanks were adjusted to be equal (80 ml/s), and sufficient to produce a thin film of water (1–2 mm deep) flowing
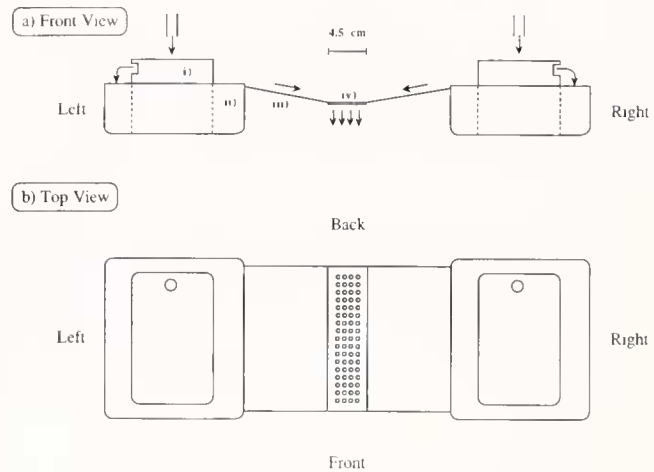

Figure 1. Schematic diagram of the choice apparatus used to assay behavioral responses of *Nucella lamellosa* individuals to various effluents: (a) front view, (b) top view. The effluent source was placed into one of the two holding tanks (i). The holding tanks emptied into header tanks (ii), which in turn emptied onto sloping, textured glass plates (iii). A thin film of water from each plate mixed on the central platform (iv) and was drained there by small holes (b). Snails were placed on the central platform with the coiling axis of their shells perpendicular to the flow of seawater.

down each plate. The holding tanks were placed within header tanks to minimize the effect of crab movement on this thin film of flowing water. Two complete apparatuses were used in two separate seawater trays oriented perpendicular to each other. Experiments were conducted under ambient light levels during the late morning and early afternoon of the day snails were collected from the field.

A trial began by placing an effluent source, either one species of crab or stones covered with barnacles, into either the right or left holding tank and allowing it to acclimatize for 20 min. The opposite holding tank contained only running seawater. Four to six *Nucella lamellosa* were tested at a time, depending on their size. Snails were placed on the perforated center platform [Fig. 1a(iv)] with their axis of coiling perpendicular to the flow of water. Adjacent snails were placed in alternating orientations, with their siphonal canal pointing either to the front or back of the apparatus. They were placed 2–4 cm apart so they were free to move without contacting each other. If two did come in contact, they were removed from the experiment.

When approximately half the snails collected for a particular trial had been tested, the effluent source was removed, the apparatus rinsed out with seawater, and the same effluent source switched to the opposite holding tank. The remaining snails were then tested as before. This procedure allowed us to test for movement biases induced by the apparatus.

To determine whether behavioral responses varied with snail size, snails were scored as either shorter or longer than 30 mm in shell length (tip of siphonal canal to apex

Table I

Statistical tests of the effects of five factors on the direction of movement by Nucella lamellosa *relative to the choice apparatus*

Effluent source	*P*-values for snails turning to right and left side of apparatus vs.:				
	a) Year of experiment	b) Seawater tray	c) Snail size	d) Snail locality	e) Snail orientation at start
Cancer productus	0.9677	0.9055	0.8743	0.7958[‡]	0.0211
Hemigrapsus nudus	ND	ND	0.9893	0.4885	0.5084
Pugettia producta	0.5488	0.5488	0.7421	0.6806	0.5141
Lopholithodes mandtii	ND	ND	0.6158	0.9202	0.2404
Balanus glandula	ND	0.5354	0.6007	0.8877[‡]	0.0040

Data were pooled from all trials with a given effluent source. *P*-values, from 2×2 contingency tables, indicate the significance of the relationship between the listed variable's states and direction of movement (to right or to left). Variables and their states are as follows: year of experiment (1989, 1990), seawater tray (A, B; trays at right angles to each other), snail size (shell length < 30 mm, shell length > 30 mm), snail locality (Grappler Inlet, Ross Islets), snail orientation at start (siphon towards front, siphon towards back of apparatus). Note that stimuli were presented from the right and left sides in roughly equal frequencies. In the interest of economy, means from all these analyses are not presented but may be obtained from the authors on request.

[‡] d.f. = 2 (*i.e.*, a third group from Grappler, acclimatized in lab, was included). ND = no data.

of shell). This length was chosen because most *N. lamellosa* shells less than 30 mm generally do not exhibit pronounced defensive traits, such as apertural teeth, which are typical of mature snails.

Since the initial orientation of each snail was known, the side of the snail exposed to the effluent source was known. The direction it turned with respect to itself (either toward the apertural lip or toward the columella) was thus also known, as well as the direction of its movement relative to the effluent source.

The direction a snail moved was scored only after its entire foot had moved off the perforated center platform and onto one of the glass plates. Snails that did not leave the platform after 45 min were noted but not included in the analyses. The average percent not responding was 12.4 ± 7.08% (n = 23) for large (>30 mm) and 5.1 ± 8.26% (n = 20) for small snails (<30 mm; mean ± SD).

Results

Tests for sources of experimental bias

Because each effluent was presented from both sides of the apparatus and from both sides of the snails at roughly equal frequencies, equal numbers should have moved to the right and left sides of the apparatus, regardless of the effluent. To determine whether the apparatus or other factors influenced turning direction, the effect of several factors on the direction moved relative to the apparatus was analyzed by 2×2 contingency tables.

With one exception, none of the potential sources of bias had a significant effect. Neither the year, the location within the laboratory, the size of snails, or source population had a significant effect on the direction of move-

ment by snails *relative to the apparatus,* regardless of the effluent (Table I, columns a–d). The effect of snail locality was tested using data pooled from three effluent sources: *Hemigrapsus nudus, Pugettia producta,* and *Lopholithodes mandtii.* Lab-acclimatized snails from Grappler Inlet ('Grappler-lab') were treated as a third locality for the analyses where *Cancer products* and *Balanus glandula* were the effluent sources.

The only detectable source of bias we observed was the starting orientation of snails, and this effect was observed only for two effluent sources: *C. productus* and *B. glandula* (Table I, column e). For *C. productus,* snails turned to the left side of the apparatus more frequently than expected when the siphonal canal faced the front (58.0 *vs.* 50%). Similarly, more snails turned toward the right side of the apparatus than expected when the siphonal canal faced the back (54.1 *vs.* 50%). In other words, most snails turned toward the apertural lip, because the lip is on the left side when viewed from the siphonal canal. The same trend was observed with *B. glandula* effluent: 55.8% turned toward the left of the apparatus if started facing front, and 62.6% turned toward the right if started facing back.

Responses to stimuli

Specificity of behavioral responses. The behavioral responses of *N. lamellosa* depended on the stimulus (Table II; see also Fig. 3 below). Significant numbers moved away from the effluent in at least one trial for each of the five different *C. productus* individuals tested. Two individuals of *C. productus* were used twice, but exposed to different source populations of snails. In sharp contrast, significant numbers of snails were attracted to the effluent of *H. nu-*

Table II

Behavioral responses of Nucella lamellosa *to effluent from five crustaceans*

Effluent source			Source on right		Source on left		
Species	Wet weight (g)	Snail locality	Snails to right	Snails to left	Snails to right	Snails to left	χ^2
Cancer productus	325.5	Grappler	7	14	16	9	4.29*
	337.4	Grappler	6	13	15	7	5.46*
	337.4	Ross	9	19	25	20	3.80[+]
	575.1	Grappler	7	7	7	7	0.00
	575.1	Grappler-lab[§§]	7	20	15	5	11.11***
	535.2	Grappler	12	25	24	14	7.09**
	339.3	Ross	5	18	16	6	11.75***
Hemigrapsus nudus	206.4[†]	Grappler	13	6	8	15	4.71*
	206.4[†]	Ross	21	15	13	24	3.95*
	175.9[†]	Grappler	23	11	14	22	5.80*
Pugettia producta	148.8[‡]	Grappler	11	10	11	12	0.09
	125.1[‡]	Grappler	10	11	11	9	0.22
	125.1[‡]	Ross	22	20	11	14	0.44
	137.9[‡]	Ross	8	14	8	6	1.50
Lopholithodes mandtii	440.5	Grappler	10	11	11	12	<0.01
	440.5	Ross	11	10	10	14	0.52
Balanus glandula	—[§]	Grappler	17	12	12	13	0.61
	—	Grappler	11	10	12	13	0.09
	—	Ross	14	12	15	9	0.38
	—	Ross	10	12	12	8	0.89
	—	Grappler-lab[§§]	9	3	7	8	2.22
	—	Grappler-lab[§§]	7	7	5	7	0.18

The effluent source was placed on either the right or the left of the snails in the choice apparatus, and each snail was scored according to the direction that it moved. Chi-square values resulted from comparing 'Source on right' and 'Source on left' data by means of a 2×2 contingency table (df = 1 for all tests).

[+] $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

[†] Combined weight of 20 crabs. [‡] Combined weight of three crabs.

[§] Weights of barnacles were not known for each experiment (100–150 individuals). [§§] Snails were acclimatized in the laboratory in running seawater with food for four days.

dus. Two different groups of *H. nudus* were used, and both attracted *N. lamellosa.* However, snails neither avoided nor were attracted to the effluent from three different groups of *P. producta,* six different groups of *B. glandula,* and the one *L. mandtii. L. mandtii* was thus the only stimulus for which we did not have more than one independent source.

Effects of manipulated variables on responses to effluent sources. Neither the year of experiment (Table III, column a), seawater tray (column b), nor snail size (column c) had a significant effect on patterns of movement relative to the effluent source. However, the direction that snails turned with respect to themselves depended significantly on the presence of effluent when *H. nudus* was the source (column e): among snails that turned away from *H. nudus,* 68.7% turned aperturally. That is, even though most snails turned toward *H. nudus,* those that turned away were more likely to do so if their apertural lip originally faced away from the stimulus.

To assess the extent of the apparent turning bias (column e, Tables I and III), the proportion of all snails that turned aperturally, regardless of the side of origin of the effluent, was tested against the proportion expected if turning was random. Out of 1026 snails, significantly more (54.9%) turned aperturally than expected (50%; $\chi^2 = 4.93$, df = 1, $P < 0.05$). This percentage (54.9%) was thus used as the percentage of snails expected to turn aperturally in the Chi-square tests of Figure 2.

When the effluent from *C. productus* arrived from the apertural side, significantly fewer snails than expected turned aperturally (Fig. 2, $P < 0.01$), whereas significantly more turned aperturally when the effluent came from the columellar side ($P < 0.01$). Conversely, more snails turned aperturally than expected when *H. nudus* effluent approached from the apertural side, though this was not quite significant statistically (Fig. 2, $P < 0.1$), and significantly fewer snails turned aperturally when effluent came from the columellar side ($P < 0.05$). The proportion of

Table III

Statistical tests of the effects of five factors on the response of Nucella lamellosa *to the effluent from five crustaceans*

	P-values for snails turning towards and away from effluent source vs.:				
Effluent source	(a) Year of experiment	(b) Seawater tray	(c) Snail size	(d) Snail locality	(e) Direction snail turned with respect to itself
Cancer productus	0.3029	0.9859	0.7333	0.3756‡	0.2760
Hemigrapsus nudus	ND	ND	0.3111	0.6249	0.0009
Pugettia producta	0.1580	0.1580	0.5570	0.9888	0.8507
Lopholithodes mandtii	ND	ND	0.4388	0.5996	0.8626
Balanus glandula	ND	0.9815	0.3437	0.2813‡	0.4106

Data were pooled from all trials with a given effluent source. P-values, from 2 × 2 contingency tables, indicate the significance of the relationship between the listed variable's states and *N. lamellosa* responses (towards or away from effluent source). See Table 1 for variable states except column e (to apertural lip, or to columella). See Figure 3 for sample sizes and means for snail locality. The remaining means from these many analyses are not presented in the interest of economy, but may be obtained from the authors on request.

‡ d.f. = 2 (as for Table 1). ND = no data.

snails that turned aperturally when the effluent sources were *P. producta, L. mandtii,* and *B. glandula* were not significantly different from expected. Thus, incorporating the bias introduced by starting orientation had no effect on the results.

Differences between populations of snails

Nucella lamellosa from Grappler Inlet, the Ross Islets, and lab-acclimatized snails from Grappler Inlet, all exhibited a statistically significant avoidance of *C. productus* effluent (Fig. 3, Table II). Those from the Ross Islets exhibited as strong a response as those from Grappler Inlet.

The proportion of lab-acclimatized snails that avoided *C. productus* was larger than that of freshly collected snails but was less significant statistically because of the smaller sample size.

N. lamellosa individuals from both localities were clearly attracted to the effluent from *Hemigrapsus nudus* (Fig. 3). Snails from the Ross Islets exhibited a stronger response ($P < 0.001$) than those from Grappler Inlet ($P < 0.05$). Neither of the two populations turned preferentially relative to the effluent from *P. producta, L. mandtii,* or *B. glandula.* Although lab-acclimatized snails from Grappler Inlet turned toward the effluent of *B. glandula* more frequently than freshly collected snails, this preference was not significantly different from 50.0%.
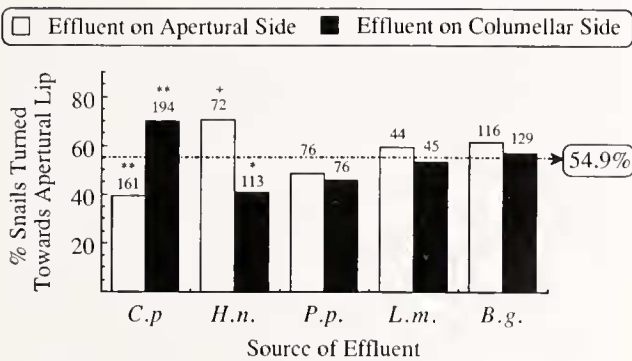

Figure 2. Behavioral responses of *Nucella lamellosa* individuals to the effluent from five different crustaceans. Snails received effluent in a choice apparatus from either the apertural or columellar side of their shells. Responses were pooled across all trials for each stimulus. The percent of snails that turned aperturally in response to a given effluent was compared by means of a Chi-square test to the percentage of all snails that turned aperturally (54.9%). *C.p.* = *Cancer productus,* *H.n.* = *Hemigrapsus nudus,* *P.p.* = *Pugettia producta,* *L.m.* = *Lopholithodes mandtii,* *B.g.* = *Balanus glandula.* +$P < 0.1$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Numbers above bars are sample sizes.
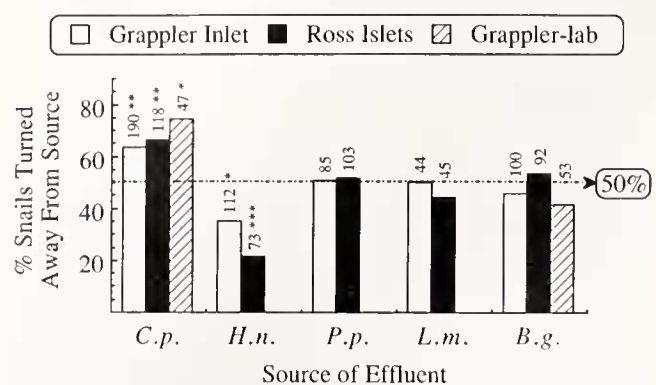

Figure 3. Avoidance responses of *Nucella lamellosa* individuals from two localities to various effluents. A third group of snails was acclimatized in the laboratory for one week with food ('Grappler-lab'). Snails were scored as moving either toward or away from each effluent source in a choice apparatus, and responses were pooled across all trials for each stimulus. The observed number of snails that turned away from each effluent source was compared by means of a Chi-square test to the number expected if they had turned at random (50.0%). Abbreviations and symbols as in Figure 2.

Discussion

Potential sources of experimental bias

Of the many possible sources of experimental bias we examined, only one had a statistically significant effect, and the effect was small. The preference of *Nucella lamellosa* to turn towards the apertural lip was slight, and appeared to have little effect on statistical inference whether incorporated in the analysis (Fig. 2) or ignored (Table II, Fig. 3). Although other explanations are possible, our handling protocol seems most likely to have been responsible for this turning bias. To standardize starting orientation, snails were placed with the coiling axis perpendicular to the flow of water. However, because the foot emerges from the apertural side, its long axis would generally have pointed toward one side of the apparatus, and snails thus may have been more likely to move in that direction.

Another possible source of bias in our experiments was the wet mass of stimulus used, because different responses to different species of crabs might have arisen as an artifact of differences in crab biomass. Biomass differences, however, seem unlikely to have influenced our results for two reasons. First, although the wet masses of *Pugettia producta,* for which no significant preference was detected, were the lowest of all crabs tested (125.1–148.8 g), the wet mass of *Lopholithodes mandtii* was the second highest (440.5 g), and no turning preference was observed for this stimulus either. Second, different sized *C. productus* individuals had no consistent effect on the magnitude of turning preference we observed: the largest crab (575.1 g) was associated with one highly significant response and one nonsignificant response, and the two most significant responses occurred with crabs of quite different size (575.1 and 339.3 g; Table II).

Responses to stimuli

Adaptive significance of a behavioral response to shell-breaking predators. The morphological responses of gastropods to shell-breaking predators have been well studied in both ecological and evolutionary time. The shell form of thaidine gastropods varies rather dramatically among local populations, and empirical evidence suggests that thick shells, characteristic of quiet-water shores, reduce vulnerability to predatory crabs (Kitching *et al.,* 1966; Hughes and Elner, 1979; Palmer, 1985). Defensive attributes of these shells can also be amplified by substances diffused from predatory crabs (Appleton and Palmer, 1988; Palmer, 1990). Geographic variation in shell morphology suggests that predation intensity increases toward tropical latitudes (Vermeij, 1978; Palmer, 1979; Bertness and Cunningham, 1981). Finally, shell-breaking predators appear to have been an important source of mortality as far back as the mid Palaeozoic (Signor and Brett, 1984) and appear to have increased in importance throughout the Mesozoic (Vermeij, 1977).

In contrast to the extensive studies of shell morphology, the behavioral responses of gastropods to highly mobile shell-breaking predators has received very little attention, presumably because the passive defense provided by the shell is usually considered the only option. Thicker shells, however, entail a greater cost (Palmer, 1981). Geller (1982) suggests that the lightly armored *Tegula funebralis* has evolved an avoidance response to a predatory crab as compensation for having a relatively thin shell. Our results indicate that *N. lamellosa,* a temperate species capable of secreting very thick shells, has also evolved a similar behavioral adaptation.

Although slow by comparison to the speed of their predators, the behavioral defenses of *N. lamellosa* may nonetheless still reduce their vulnerability. An avoidance response, if adaptive, functions to reduce the probability of encounter between predator and prey. Hence, it does not necessarily require quick movement. Its effectiveness would presumably increase as the distance to which the prey could detect the predator increased. Furthermore, in the heterogeneous environment of rocky shores, a refuge may be only a few centimeters away, also reducing the need for a dramatic response.

Adaptive significance of specificity. The avoidance of crabs by *N. lamellosa* appears to be specific to predatory species. Predator-specific defensive behaviors have been observed in other gastropods in response to both predatory asteroids and gastropods (Edwards, 1968; Phillips, 1976; Hoffman, 1980), and have also been observed in barnacles (Palmer *et al.,* 1982), anemones (Lawn and Ross, 1982), and echinoderms (Shaw and Fontaine, 1990). Such specificity presumably evolves because avoidance behaviors are costly in terms of time lost from foraging. Dogwhelks, for example, require from several hours to a day to handle a single barnacle (Dunkin and Hughes, 1984) or mussel (Hughes and Dunkin, 1984). Time spent retreating to and remaining in a refuge in response to a distant predator could otherwise be used for foraging. Avoidance behaviors should thus evolve to a level of specificity that minimizes inappropriate responses. Numerous studies suggest that invertebrates can weigh these tradeoffs between risk and reward while foraging (Sih, 1986; Burrows and Hughes, 1989).

The attraction of *N. lamellosa* to the scent of *Hemigrapsus nudus* was initially quite puzzling, because large *H. nudus* can break the shells of small *Nucella* in the laboratory (V. Ash and A. R. Palmer, unpub. obs.). This attraction was observed in three separate experiments with snails from two different populations (Table II) and hence was not a sampling artifact. On reflection, we feel this attraction may have a rather intriguing explanation. Be-

cause snails rely on olfaction as their primary sensory mechanism (Kohn, 1961), *N. lamellosa* may use the water-borne cues released by *H. nudus* to locate potential refugia, such as crevices or the undersides of boulders, from a distance. Without such distance chemoreception, snails would have to rely either on local cues encountered through random movement (*e.g.*, rapidly changing light levels or reduced water movement) or on their ability to retrace a path back to a refuge left earlier. Because *H. nudus* commonly occurs in crevices and under rocks on almost any rocky shore in the northeastern Pacific (Kozloff, 1987), they would consistently be associated with potential refugia. Although *N. lamellosa* might possibly have been attracted to what was perceived as a 'familiar' scent in the unfamiliar surroundings of the laboratory, the lack of an attraction to barnacles (Table II) would seem to rule this out.

The lack of a response to barnacles, common prey for *N. lamellosa*, was surprising. The experimental procedure was designed to minimize the effects of the laboratory on snail behavior by using animals as soon as they were brought back from the field. However, this procedure may have been mildly stressful, and may thus have suppressed normal foraging behaviors. Snails that experienced the slight 'trauma' of being detached and handled may have only been sensitive to risk-related stimuli rather than foraging-related stimuli.

Differences between populations

Nucella lamellosa individuals from the protected shores of Grappler Inlet have thick shells with pronounced apertural teeth, whereas those from the Ross Islets, a site of intermediate wave exposure, have much thinner shells and less pronounced apertural teeth (Appleton and Palmer, 1988). These large morphological differences imply very different predation regimes. Geller (1982) reported that *Tegula funebralis* from a site where crabs were absent did not show an avoidance behavior, while those sympatric with crabs did. Although we did not include a site where predatory crabs were totally absent, we found that snails from these two sites of presumably quite different predation intensity nonetheless responded similarly to the scent of *C. productus*. This result parallels others for *N. lamellosa* from the same two localities, where snails altered their morphology in an adaptive manner when exposed to the scent of *C. productus* over longer periods of time (Appleton and Palmer, 1988). Thus the ability of snails from both localities to distinguish between predatory and non-predatory crabs is not surprising.

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